MADROÑO

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SOME TAXONOMIC AND ECOLOGICAL CONSIDERATIONS OF THE GENUS MARAH (CUCURBITACEAE)

KENNETH M. STOCKING

In 1834 Hooker listed specimens collected near the Columbia River by Scouler and Douglas as *Sicyos angulatus*. Although only staminate flowers were collected, we can speculate that this record may be the first made of any species of *Marah*. Torrey and Gray in 1840, using Scouler's and others' specimens, designated these Columbia River plants as *Sicyos oreganus*. Kellogg in 1855, noting the "gigantic fleshy roots" and other differences between a San Francisco cucurbit and all others, named his San Francisco plant *Marah muricatus*. We now recognize both Torrey and Gray's and Kellogg's specimens as *Marah oreganus*. Some early botanists, notably Sereno Watson, rejected Kellogg's name, even though it was accompanied by a complete description, because the name first appeared in a newspaper. Naudin, in 1859, described a plant grown in the botanical gardens in Paris from a large root from California, and named it *Echinocystis fabacea*. In 1876, Watson, in describing a member of this genus under the name *Megarrhiza guadalupensis,* used a *nomen nudum* of Torrey. Cogniaux in 1881 made *Marah* one of three sections of *Echinocystis*. Edward Greene in 1890, noting Rafinesque's 1808 name, *Micrampelis,* placed all the Marahs he knew in that inadequately described genus.

Others who have contributed to the taxonomy of the genus *Marah* are: J. W. Congdon, who named the species *horridus* and studied related species, and W. L. Jepson, who in his Manual and Flora shows a better understanding of the group than any of the above mentioned persons.

MORPHOLOGY

GERMINATION. *Marah* alone among the genera *Marah, Echinocystis,* and *Echinopepon* has hypogeous germination. In order to compare the germination of the five species of *Marah* for which seeds were collected, the author stratified them by placing them in moistened, but not saturated, peat moss in refrigeration at temperatures of from five to ten degrees centigrade. With this method there was a high percentage of germination in *M. fabaceus* var. *agrestis, M. horridus, M. macrocarpus* var. *typicus, M. oreganus,* and *M. watsonii* (fig. 1). To determine whether stratification at low temperatures is necessary, controls without refrigeration were maintained. None of these seeds germinated; so one may conclude that low temperature is necessary for normal germination of these species of *Marah*.

The hypogeous method of germination was found to obtain in each of the five above-mentioned species. In every case the two cotyledons, which appear as a root-like organ, are protruded through the seed coat for a

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distance of from 3.2 to 11 cm. As the cotyledon structure elongates, the two cotyledons become separated near their distal ends; the epicotyl, which soon is recognizable as a branching shoot, grows upward; and the hypocotyl, which rapidly develops into the tuber and taproot, grows downward. The effect of this type of germination is early placement of the tuber deep in the soil where frost is rare or lacking.

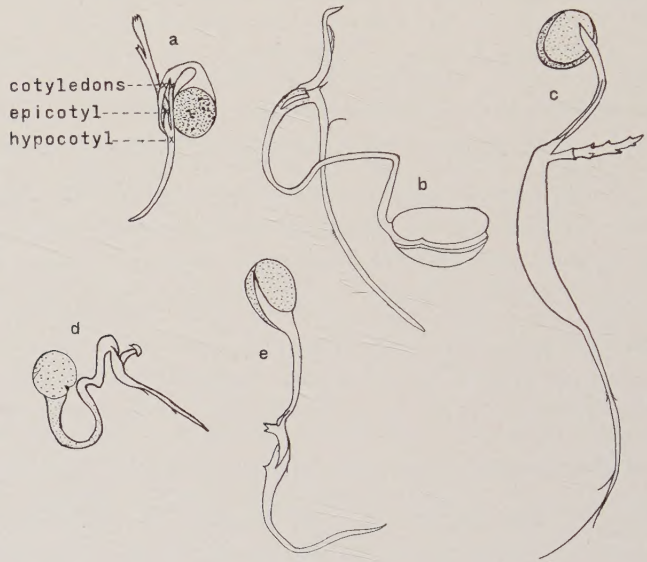

FIG. 1. Early stages in germination of *Marah* seeds; *a, M. macrocarpus* var. *macrocarpus; b, M. horridus; c, M. oreganus; d, M. watsonii; e, M. fabaceus* var. *agrestis.*

ROOTS AND TUBERS. Tubers have been observed to develop from the hypocotyl in *Marah fabaceus, M. horridus, M. macrocarpus, M. oreganus,* and *M. watsonii.* The writer has not germinated seeds of *M. gilensis* or *M. guadalupensis.* During the first five years tubers have been seen to have a shape which tapers above toward the stem base and less abruptly below toward the tap root. From a study of numerous more mature tubers of the above mentioned species which the author has dug out and replanted, it can be conservatively estimated that the tubers remain fusiform for several to many years. As tubers mature, they become more globose. Some of the heaviest specimens dug, especially those of *M. macrocarpus,* had a greater diameter than length. These were growing where rocks limited downward growth of large organs. The basal portion of one large tuber of *M. horridus* was split so that it somewhat resembled the legs of a man. The heaviest tuber dug by the author weighed 58 kg. (fig. 2). One has been reported to weigh about 90 kg. (Science News Letter, 1948).

Beneath the bark, which becomes quite rough and thick in old tubers,

lies the large, bulky area of starchy parenchyma which contains concentric rings of xylem vessels. (In digging to locate the tubers, the author knows, when he smells an odor like that of fresh-cut potatoes, that he has cut into a tuber.) The core of old tubers is dark, hard, and without starch. The concentric rings in the starchy parenchyma are not well enough defined to allow a very accurate estimate of age; however, the author did estimate the age of the 58 kg. specimen (fig. 2) to be fourteen years. In one growing season and in adverse light conditions, one tuber of *M. fabaceus* var. *agrestis* reached a length of 13 cm. and a diameter of 1.7 cm.

FIG. 2. Tuber of *Marah fabaceus* var. *agrestis* from Linden, California: weight, 58 kilograms; estimated age, fourteen years.

Numerous lateral roots arise along the tuber. On large specimens, these are of sufficient size to have considerable storage function.

The tap roots in plants only a few years old are approximately as long as the tuber and are still fusiform. As the plant ages, lateral roots approximate or surpass the diameter and length of the tap root. Dr. Flora M. Scott (1943) has found that the transition to root structure occurs near the base of the storage region, the tuber presumably developing from the hypocotyl and stem base. The upper 20 cm. portion of a 65 cm. long tuber of *M. fabaceus* var. *agrestis* was cut off and the remainder left rooted in the ground. Healthy shoots grew from an area on the upper edge of the rooted portion.

GEOGRAPHICAL DISTRIBUTION AND INTER-RELATIONSHIPS OF THE SPECIES OF MARAH

Marah oreganus has a range wider than that of any other species of the genus. It may be considered primitive in its possession of relatively large calyx lobes and of a comparatively spine-free fruit. *Marah guadalupensis*, a little-collected species, and one which may now be extinct because of the goats which have overrun the island of Guadalupe, has flowers and fruit very much like *M. oreganus*, and may be the closest relative of *M.*

oreganus. The range of *M. Watsonii* is adjacent to that of *M. oreganus*, and its flowers, fruits, and seeds are so much like those of *M. oreganus* that one may well speculate that *M. watsonii* is a second species which was derived from *M. oreganus*.

Marah fabaceus is a third possible species which may have been derived from *M. oreganus*. In its geographical position and morphological characteristics it lies between each of the two pairs of species: *M. oreganus-M. gilensis*, and *M. horridus-M. macrocarpus*. It is interesting to note that *M. fabaceus* var. *fabaceus* has a range nearly adjacent to that of all the species except *M. gilensis* and *M. guadalupensis*. *Marah macrocarpus* var. *major* and var. *micranthus* represent groups which only recently have been geographically isolated. *Marah macrocarpus* var. *major* needs further collecting inasmuch as the Channel Islands contain many apparent intermediates between the species and its variety.

Some General Ecological Relationships

The author has spent many hours in the field locating, observing, collecting fruits and seeds of, and digging tubers of each of the species of *Marah* except *M. guadalupensis*. In addition to the results recorded here, he has experienced loss of weight, callouses, and a severe case of poison oak. From one to four tubers of each of the following species have been transplanted to a plot of sandy soil in Fresno, California: *M. fabaceus* var. *agrestis*, one tuber; *M. horridus*, four tubers; *M. macrocarpus*, three tubers; and *M. watsonii*, one tuber. The five largest tubers, weighing between 6 and 31 kg. when dug, have grown rather well. When one tuber of *M. fabaceus* var. *fabaceus*, two tubers of *M. fabaceus* var. *agrestis*, one tuber of *M. horridus*, one tuber of *M. macrocarpus* var. *macrocarpus*, one tuber of *M. oreganus*, and three tubers of *M. watsonii* were planted in Stockton, California, even better results were obtained. All produced flowers except *M. fabaceus* var. *fabaceus*. One plant of *M. macrocarpus* and two of *M. watsonii* produced easily distinguishable mature fruits and seeds. *Marah horridus* and *M. oreganus* also produced identifiable fruits. In no case was there any appreciable change in the floral characteristics of any species. Thus under garden conditions character differences of the reproductive organs were found to remain constant in these species. The leaves of *M. horridus* and *M. oreganus* were noticeably smaller in the sunny plots than in their original shady canyon homes.

Temperature Factors. The family *Cucurbitaceae* is primarily one of the tropics and subtropics. The perennial genus *Marah* is exceptional in that it is able to prosper even at latitudes of more than 45° N. This is due to the development of deeply-buried large tubers. However, no species of *Marah* has been found growing higher than the highest elevations of the Upper Sonoran Life-Zone. Minimum temperatures here are lower than those of the habitat of *M. oreganus* in the coastal Transition Life-Zone. *Marah horridus*, at an elevation of 1500 m. near King's Canyon, *M. watsonii* near Paradise, California, and *M. macrocarpus* var. *macrocarpus*

near Mount Wilson all grow to within a few hundred meters of the edge of the coniferous forest, but none have been observed to grow in this forest. In each of these places, plants grow near or on a ridge where air drainage is excellent, where snows do not remain long, and where the ground does not freeze to tuber depth.

Moisture Factors. *Marah oreganus* is adapted to areas where the annual precipitation is more than 200 cm., while *M. macrocarpus, M. gilensis,* and *M. fabaceus* var. *agrestis* are adapted to many areas where there is less than 25 cm. of rain. The other species and varieties receive intermediate amounts of rain. Occasional snows fall in the higher ranges of all of these plants, especially those of *M. oreganus, M. watsonii,* and *M. horridus.*

Light Factors. Individual plants of all the species of *Marah* except *M. guadalupensis* have been observed by the writer to grow well both in direct sunlight and in partial shade. The latter type of environment, especially where there are shrubs or other low plants over which the Marahs twine, supports the greatest numbers of these cucurbits. The quite elongated stems and very large and relatively delicate leaves of many shade-dwelling plants of *M. oreganus* and some of *M. macrocarpus* var. *major* are striking.

All species of *Marah* blossom by late winter or early spring. *Marah watsonii* and *M. horridus* have been observed to possess open blossoms as the plants push through the soil surface. Stems of *M. macrocarpus* var. *macrocarpus,* which came through the surface of the soil in June, produced buds which did not blossom. These observations suggest that, photo-periodically speaking, all species of *Marah* are short-day plants.

Edaphic Factors. It was observed that all of the tubers dug were growing in well-drained, well-aerated soils: *M. horridus* in soils derived from decomposed granite; *M. macrocarpus* var. *macrocarpus* in the same, in gravelly soil, or in other soils on slopes; *M. watsonii* in friable soils; *M. fabaceus* in a variety of light soils; and *M. oreganus* in more or less light loam. No tuber of *M. gilensis* was dug, but the plants observed were growing in gravelly soil. After one has dug a number of tubers, he begins to associate them with friable soils, sands, gravel, and tangled masses of roots.

When one observes the depth at which the tubers are buried, he can appreciate the place of good drainage in their survival. The tuber top of *M. fabaceus* var. *agrestis* was 17 cm. below the surface of the earth less than six months after the seed germinated. Others, measured as they were dug, were: *M. horridus,* elevation 1500 m. near King's Canyon, Fresno County, California, buried 25 and 38 cm.; *M. macrocarpus* var. *macrocarpus* in the San Gabriel River wash near Arcadia, Los Angeles County, California, buried 15 and 30 cm.; and on the Angeles Crest Highway, just below the turn-off to Mount Wilson Observatory, Los Angeles County, California, and a short distance below the Transition Life-Zone, buried 30 and

38 cm. Tubers of *M. watsonii, M. fabaceus,* and *M. oreganus* were buried at comparable depths, but the exact measurements were not taken.

Acid-base relationship were, as far as yet observed, not found to be critical factors. Plants of *Marah oreganus* and *M. fabaceus* var. *fabaceus,* natives of the somewhat acid soils of the coastal *Sequoia sempervirens* forest, when transplanted to a slightly alkaline soil of the San Joaquin Valley appeared to have made a satisfactory adaptation to the change.

Plant Associates. In the coastal mountains of central and northern California both *M. fabaceus* var. *fabaceus* and *M. oreganus* have been collected by the author as they were growing over *Sequoia sempervirens* in association with *Quercus agrifolia,* and *Corylus rostrata* var. *californica. Marah fabaceus* var. *agrestis* in the foothills around much of the Great Valley of central California is associated with *Pinus sabiniana, Quercus douglasii, Quercus wislizenii, Aesculus californica,* and several shrubs, especially *Ceanothus* spp. and *Arctostaphylos* spp.; *M. watsonii* and *M. horridus* share restricted parts of this range with *M. fabaceus* var. *agrestis. M. macrocarpus* var. *macrocarpus* is associated with *Quercus agrifolia, Yucca whipplei, Rhus ovata,* and many other species of woodland and shrub-land plants of southern California. At elevations of 4,500 feet or lower, *M. gilensis,* a species of Arizona and New Mexico, is common mostly in thickets along streams.

The plant observed to be most frequently associated with most species of the genus *Marah* was *Rhus diversiloba.*

Other Plant Relationships. Individual *Marah* plants compete effectively with grasses, other angiosperms, and gymnosperms. Since growth begins very early in the season they have a real advantage over almost all other deciduous plants.

As far as has been observed, they have no natural plant parasites, except molds, and these seem to damage only plants injured in transplanting.

Animal Relationships. Very few vertebrates eat any of the vegetative parts of *Marah.* The name *Marah* is derived from the Latin word *amarus* which means bitter. Most animals respond to this bitterness as man does. Damage done by western striped and twelve-spotted cucumber beetles and by squash bugs has been observed to be of little significance except to a few new shoots. A large portion of one growing tuber had been eaten by what the author, who has investigated many gopher underground networks, considered to be a very hungry gopher. Certainly some rodent had eaten it. There is no evidence that domesticated animals browse on *Marah.* Numerous plants of several species have been observed to prosper in various well-grazed pastures.

Clearing of land and cultivation have reduced the numbers of *Marah* plants. However, very few agriculturists have been concerned enough with the "wild cucumbers" that grow along fence rows to try to eliminate them. A present threat of probably greater significance to their survival is that of their repeated poisoning by various herbicides. Fires in four burned-over areas studied appeared only to have eliminated competition for the spreading colonies of *M. fabaceus* var. *agrestis* and *M. watsonii.*

Rodents, especially the ground squirrel, *Citellus beechyi,* compete for the seeds of *Marah.* In Fresno County near Alcalde, ground squirrels were seen eating many green seeds. Undoubtedly rodents are among the most important means of seed dispersal. Gravity on steep hillsides has repeatedly been seen to be another means of seed distribution.

A number of species of small black ants have often been studied as they climbed about the flowers of *M. fabaceus* var. *agrestis* in the field. Similar ants have been observed on flowers of *M. macrocarpus* var. *macrocarpus* and *M. horridus* in the field, and on all of the cultivated species and varieties. These ants apparently find the trichomes of the stems, peduncles, and pedicels excellent ant ladders. When observed under the microscope, the ants were found to have pollen on their bodies. A few honey bees and small beetles were observed on the flowers, but never in sufficient numbers to be of much significance as pollinating agents.

Economic Importance

In the well-developed agricultural areas of California, the various species of *Marah* serve as breeding places and distribution points for various species of insect pests. On *Marah fabaceus* var. *agrestis* growing adjacent to several cultivated crops, the author has noted large numbers of colonies of the rapidly-reproducing western striped cucumber beetle, *Diabrotica trivittata,* of the twelve-spotted cucumber beetle, *Diabrotica duodecimopunctata,* and the squash bug, *Anasa tristis,* and in his garden these same insects occurred on *M. macrocarpus* var. *macrocarpus, M. oreganus, M. horridus,* and *M. fabaceus* var. *fabaceus.* E. O. Essig (1926), says that the larvae of the striped cucumber beetle commonly attack the roots of cucumbers, melons, pumpkins, squash, and other cucurbits, eating linear holes toward the bases of the plants, while the adults feed on the tops and also on beans, beets, corn, peas, sunflower, almond, apple, prune, and other plants. The larvae of the twelve-spotted cucumber beetle feed upon the roots and tubers of various plants and often do considerable damage, especially to grasses, corn, millet, oats, rye, wheat, and weeds. Adults are often serious pests feeding on many kinds of plants including fruit trees, flowers, field, forage, and truck crops. Adults and young of the squash bug do great damage to many cucurbits, and are apparently a carrier of vine wilt disease.

Because of its strong cathartic properties, a substance from the tuber of *Marah fabaceus* has been used in a laxative called Stroughton's Bitters. Another substance found in *Marah* tubers has the property of dilating the eyes. Neither of these two substances is at present being used.

The author has speculated that since various species of *Marah* have stored hundreds of pounds of starch per acre while growing in such waste places as the San Gabriel wash, Los Angeles County, and the chaparral-covered slopes of many hills of California, it might sometime be a practical plan to harvest and use this starch. It should not be difficult to leach out any poisonous substances in much the same way that manioc is treated to obtain tapioca.

Seeds of *Marah* show promise of being a valuable source of oil. The seed's contents will ignite when heated with a match.

Genetic Considerations

Hybridization. Five species of *Marah* were cultivated in a small plot within a radius of six meters; the seeds of *M. watsonii* and *M. macrocarpus* var. *macrocarpus* taken from this plot showed no signs of hybridization, nor did plants grown from these seeds. *Marah fabaceus* var. *agrestis* and *M. watsonii,* growing within a few feet of each other near Placerville, California, the type locality of the latter, also show no signs of interchange of genes between species. *Marah fabaceus* var. *fabaceus* and *M. oreganus* grow close together in the *Sequoia sempervirens* forest near Pescadero, California; *M. fabaceus* var. *agrestis* and *M. horridus* are found in close proximity in the woodland near Bagby, California, yet each of these species has been observed to remain morphologically distinct. A study of the distribution maps of *Marah* (fig. 5) shows other areas shared by more than one species. The author has yet to find evidence of any interspecific hybridizing among specimens which have been collected in flower and fruit. Apparent intergrades between varieties are rather common, however, especially between *M. fabaceus* var. *fabaceus* and *M. fabaceus* var. *agrestis* in central California and between *M. macrocarpus* var. *macrocarpus* and *M. macrocarpus* var. *major* on the Channel Islands.

Specimens of reddish-seeded races of *M. macrocarpus* var. *macrocarpus,* growing in the San Gabriel River wash near Arcadia, California, and of *M. fabaceus* var. *agrestis* at a point east of Linden, California, have been found by the author. A specimen of *M. oreganus* (*Tracy 3532* UC) and one of *M. watsonii* (*Heller 11812* CAS, DS, UC) likewise represent red races.

Chromosome Considerations. McKay (1931) found 32 to be the diploid chromosome number of *M. macrocarpus, M. fabaceus,* and *M. oreganus.* Whitaker (1949) also obtained a chromosome count of 32 for *M. macrocarpus.*

Generic Relationships

The closest relatives of *Marah* are apparently *Echinopepon* and *Echinocystis.* One may speculate that the genus *Echinopepon* is the oldest of these three genera. It ranges from central Argentina to New Mexico and Arizona, and may have given rise to the genus *Echinocystis. Echinocystis,* found chiefly in the northeastern parts of the United States and adjacent parts of Canada, in addition to having many floral characteristics in common with *Echinopepon* is, like it, an annual, with epigeous germination. *Marah* may have been derived from *Echinocystis* in the eastern part of the Columbia Plateau in the Snake River region. *Marah* is more like *Echinocystis* in its irregular method of dehiscence and its seed size than it is like *Echinopepon.* It is unlike either *Echinopepon* or *Echinocystis* in being a perennial with large tubers and in having hypogeous germination.

In the vegetative condition, species of the three genera mentioned above, and, in addition, those of *Brandegea* and *Vaseyanthus* are often confused. They may be separated readily, however, on the basis of flowering and fruiting characters (Stocking, 1955, p. 84, key). The range of the genus *Brandegea* coincides with that of the northwestern part of the range of *Echinopepon* and the southern part of the range of *Marah;* that of *Vaseyanthus,* with the western part of the range of the genus *Echinopepon,* especially in Lower California.

Taxonomic Considerations

The type specimens of some of the species of *Marah* were destroyed by the San Francisco fire of 1906 or in other ways. In these cases lectotypes have been suggested. All measurements recorded, except those of floral parts and stem length, were made of dry materials. Flowers of the five species of California *Marah* were preserved in dilute formalin; flowers of all other species were boiled in water. Where measurements of fresh and variously preserved materials were compared, no significant differences were observed. Stem length of the California species of *Marah* was taken in the field. Only mature seed measurements are given since the light-colored immature seeds of *Marah* are noticeably larger than the mature seeds. Specimens cited in this study were assembled in the herbarium of the University of Southern California, Los Angeles. Abbreviations used in citations are those proposed by Lanjouw (1954). In addition, KMS refers to the private herbarium of the author and USC refers to University of Southern California.

Marah Kell. Proc. Calif. Acad. ser. 1 (1): 38. 1855. Type: *M. muricatus* Kell. [now known as *M. oreganus* (Torr. & Gray) Howell, Dunn in Kew Bull. 4: 145. 1913]. *Megarrhiza* Torr. Pacif. R. Rep. 6, part 3, number 2: 74. 1858, *nomen nudum;* Pacif. R. Rep. 12, part 2, number 3: 61. 1861, based on *Sicyos oreganus* Torr. & Gray, Fl. N. Am. 1: 542. 1840. *Echinocystis* (section Marah) Cogn. in Monogr. Phan. 3: 816. 1881, based on *Marah muricatus* Kell. Proc. Calif. Acad. ser. 1 (1): 38. 1855.

Plants sub-glabrouse to somewhat vestite, climbing or trailing, monoecious, with deeply striated annual stems arising from 1 to 5 "necks" on large, fusiform or globose, perennial tubers. Leaf blades suborbicular, cordate, more or less deeply 5–7-lobed or cleft; basal sulci narrow and closed to sometimes broad and opened; tendrils unifid to trifid on peduncles somewhat shorter than petiole length; petioles 0.5–1 times leaf diameter. Staminate flowers in racemes or panicles, axillary, tardily deciduous; pedicels persistent; calyx teeth small or obsolete, alternate with corolla lobes; corolla campanulate or rotate, inserted on the calyx, the surfaces, especially the upper, more or less glandular and with trichomes, usually 5– (4–8-) merous; 3 (–4) anthers fused into a cylindrical or somewhat flattened globose head; filaments a fused column. Single pistillate flower from same axil as staminate inflorescence and commonly

larger than staminate flower; stigma discoid to sub-globose, style short or nearly obsolete; ovary (2–) 4 (–8) celled, ovules 1–4 per cell. Mature fruit a turgid capsule, globose-ellipsoidal or broadly fusiform, pendant, its spines large and numerous to small and almost lacking, irregularly dehiscent at or near the apex, the ripe seeds falling or being ejected through a jagged opening left by splitting or dropping of the beak; dry fruit yellowish-brown, sometimes with mature seeds held by septae for several months. Seeds large; commonly brownish-grey, olive, or tan; cotyledons large; seed coat thick-walled, lignified, suberized.

Key to the Species

1. Corollas of all mature flowers rotate or only slightly cup-shaped.
   2. Corollas of all flowers slightly cup-shaped, white; fruit oblong-cylindrical, ovules more than 4; southern California and Lower California . . . . . 6. *M. macrocarpus*
   2. Corollas of all flowers rotate, fruit globose, ovules 4 or fewer.
      3. Staminodia present in pistillate flowers; flowers white or nearly so; Arizona, New Mexico . . . . . 7. *M. gilensis*
      3. Staminodia absent in pistillate flowers; flowers yellowish-white; California . . . . . 4. *M. fabaceus*
1. Corollas of all mature flowers campanulate.
   2. Staminate flowers less than 8 mm. in diameter; ovary, fruit, and seeds globose; leaves glaucous beneath, deeply dissected; northeastern California . . . . . 3. *M. watsonii*
   2. Staminate flowers more than 8 mm. in diameter; ovary and fruit elongated.
      3. Calyx teeth more than 1 mm. long; linear-lanceolate; Guadalupe Island, Mexico . . . . . 2. M. *guadalupensis*
      3. Calyx teeth less than 1 mm. long; deltoid to subulate-lanceolate.
         4. Ovaries and fruit ovate; spines inconspicuous; seeds discoid; humid Pacific Northwest . . . . . 1. *M. oreganus*
         4. Ovaries and fruit cylindrical, spines conspicuous; seeds cylindrical; foothills and mountains around southeastern San Joaquin Valley . 5. M. *horridus*

1. Marah oreganus (Torr. & Gray) Howell, Fl. NW. Am. 1: 239. 1898. *Sicyos oreganus* Torr. & Gray, Fl. N. Am. 1: 542. 1840. Type: "on the Oregon (Columbia River, from near its mouth to Kettle Falls: Dr. Scouler, Douglas, Mr. Tolmie," Scouler (NY! photograph KMS!). *Megarrhiza oregona* Torr. Pacif. R. Rep. 12, part 2, number 3: 61. 1861. *Echinocystis oregona* (Torr. & Gray) Cogn. Mem. Acad. Sci. Belg. 28: 87. 1878. *Micrampelis oregona* (Torr. & Gray) Greene, Pittonia 2: 129. 1890.

Marah muricatus Kell. Proc. Calif. Acad. ser. 1, 1: 38. 1855. Type: "declivities of the hills back of the Mission Dolores, on Mr. Hutchinson's ranch near San Francisco," (specimen did not survive the San Francisco fire of 1906). *Echinocystis* (section Marah) *marah* Cogn. Monogr. Phan. 3: 817. 1881, based on *Marah muricatus* Kell. *Micrampelis marah* (Cogn.) Greene, Pittonia 2: 129. 1890.

It might be noted that Torrey and Gray first used the specific name *oreganus* in 1840 and that it agrees with the masculine name *Marah*.

Aerial stems from 1 the first year to 12 in older plants, 2–5 mm. in diam., 1–7 m. long, sparsely pubescent to sub-glabrous, internodes 5–15 cm. long; leaf blade sub-orbicular, 8–20 (–35) cm. in diam. with broad, rounded sinuses between the 5–7 more or less shallow lobes, the base of blade cordate, apex of terminal lobe acute, often acuminate, others obtuse or acute, the margin of blade entire, sub-undulate, sub-crenulate to denticulate, the surfaces sub-glabrous to sparsely pubescent; petiole (2–) 4–8 (–12) cm. long, pubescent; tendrils trifid or bifid, the peduncle heavy, 2–7 cm. long; staminate flowers in racemes, rarely in panicles, the racemes 10–30 cm. long with 5–20 flowers, seldom more than 10 mature flowers open at one time, on pedicels 5–12 (–20) mm. long, the calyx lobes broadly triangular to subulate, to 0.67 mm. long and 1 mm. wide, with conspicuous trichomes sometimes present at apices, the corolla campanulate, 10 mm. long, 12–15 mm. in diam., white, basal part somewhat greenish, its lobes oblong-ovate, 5–6 mm. long, 2–4 mm. wide at base, with apices obtuse, the stamens with anther head cylindrical, 2–2.5 mm. in diam., slightly longer than wide and with apex flattened, the 5 anthers inverted, U-shaped, with filament column 2 mm. long; pistillate flower with calyx lobes deltoid, subulate, or filiform, to 1 mm. long, the corolla campanulate, 15–17 mm. in diam., its lobes oblong, unequal, 8–10 mm. long, 3–4 mm. wide at base, and with apices acute, the staminodia more or less adherent to style, the stigma broadly obconic and 3 mm. in diam., the style to 3 mm. long and 2 mm. in diam.; immature fruit oblong-ovate, mature fruit ovate, attenuate at both ends, 4.5–6.5 (–8) cm. long, 3–4 (–4.5) cm. in diam., with alternating broad longitudinal, darker and lighter bands of color, the spines few, weak or almost lacking, to 6 mm. long, the peduncle 2–3 (–3.5) cm. long, the carpels 2–3, each with 1–2 (–4) ovules, these often inclined toward the apex from the horizontal; seeds discoid, surfaces slightly undulating, 16–20 mm. in diam., 8–12 mm. thick, with conspicuously ridged hilum 4–6 mm. long and 0.5–1 mm. high, dark reddish-brown, encircled with inconspicuous, slightly grooved line.

Humid Pacific Coast areas from San Mateo and Santa Clara counties in California to southern Vancouver Island in British Columbia, inland especially along waterways, as far east as the Snake River valley in eastern Oregon (fig. 5).

Representative specimens seen. CALIFORNIA. Alameda County: Oakland Hills, May, 1881, *Rattan 49619* DS; Glenn County: summit of ridge north of Black Butte, July 13, 1944, *Howell 19758* CAS. Humboldt County: south of point of Cape [Mendocino], May 20, 1933, *Tracy 12227* DS, GH, UC, US. Marin County: Tamalpais, *Brandegee,* DS 7502; wooded hillside 3.3 miles east of Dillon Beach, March 29, 1947, *Stocking 19* KMS, USC. San Mateo County: common about the hills, April 4, 1902, *Baker 450* DS, GH, POM, UC, US; *Sequoia sempervirens* forest, 1.5 miles east of Pescadero, May 15, 1947, *Stocking 40* KMS, USC. Santa Clara County: Black Mountain, May, 1903, *Elmer 4733* ARIZ, DS, UC, US. OREGON. Benton County: northeast of Corvallis, May 22, 1917, *Anderson* USC; near bank of Snake River at landing, east Oregon, May 27, 1901, *Cusick 2523* GH, UC, US. WASHINGTON. Klickitat County: Grand Dalles, March 26, 1934 *Jones 4461* CAS. Snohomish County: Marysville, May,

1928, *Grant* USC. BRITISH COLUMBIA. North Saanich, Vancouver Island, July 10, 1917, *Newcombe* UC.

The race with reddish seeds collected at Eureka (*Tracy 3532* UC) might well be further investigated.

2. MARAH GUADALUPENSIS (Wats.) Greene, Leafl. Bot. Obs. 2: 36. 1910. *Megarrhiza guadalupensis* Wats. Proc. Am. Acad. 2: 138. 1876. Type: Guadalupe Island, growing on high rocks. 1875. *Palmer 33* (GH! photographs KMS! fig. 3, isotypes GH! US!). *Echinocystis guadalupensis* (section *Marah*) *guadalupensis* (Wats.) Cogn. Monog. Phan. 3: 819. 1881. *Micrampelis guadalupensis* (Wats.) Greene, Pittonia 2: 129. 1890.

Stem to 3.5 mm. in diam., glabrous to puberulent, internodes 5–20 cm. long; leaf blade broadly orbicular to ovate, (10–) 15–20 (–25) cm. in diam., broadly 5-lobed, the lobes triangular-ovate to oblong, acute or obtuse, the basal sulcus of blade 3–6 cm. deep, narrower to wider than deep, the margin of blade sinuate to denticulate or somewhat dentate, the upper surface slightly papillate-scabrous, minutely pubescent, especially on veins, the lower surface more nearly glabrous; petiole 5–8 (–10) cm. long, sub-glabrous to puberulent; tendrils bifid or trifid, the peduncle rather rigid, 3–5 (–8) cm. long; staminate flowers in raceme or panicle 10–20 (–30) cm. long with 6–12 flowers per raceme and up to 6 racemes per panicle, on pedicels 3–8 mm. long, the calyx lobes linear-subulate, 1.5–2 mm. long, 0.5–0.8 mm. broad at the base, the corolla broadly campanulate, 12–20 mm. in diam., its tube 4–5 mm. long, its lobes unequal, triangular-oblong, 6–7 mm. long, 3–5 mm. wide at base, sub-obtuse, with margins and inner surfaces glandular-punctate with stalked glands, the stamens with anther head sub-globose, 2.33 mm. in diam., thecae irregularly contorted, the filament column 1.5 mm. long, .06 mm. in diam.; pistillate flower 18–24 mm. in diam., with calyx lobes linear, 6–7 mm. long, 0.33 mm. wide at base, the corolla open-campanulate, its tube 1.67–2 mm. long, its lobes oblong-lanceolate, 8–10 mm. long, 2–4 mm. wide at base, obtuse, the stigma thickened, discoid, 2.5 mm. in diam., 0.67–1 mm. thick, the staminodia occurring under stigma edges, subulate, 0.5 mm. long, 0.17 mm. in diam., the style 0.33–0.67 mm. long, 0.33 mm. in diam.; fruit ovoid, short beaked, 6 cm. long, 5 cm. in diam., striated from base to apex, short pubescent, its spines weak, 1–3 mm. long, 0.25–0.5 mm. in diam. at base, glabrous to puberulent; peduncle 6–8 cm. long, puberulent; seeds 2, ovoid-lenticular, 28 mm. long, 25 mm. wide, 14 mm. thick (when slightly immature), olivaceous, circumferential line inconspicuous.

Known only from Guadalupe Island off the west coast of Baja California, Mexico, latitude 29° N., longitude 118° W.

Representative specimens seen. March-June, 1897, *Anthony 234* GH, POM, UC, US; March 25, 1897, *Brandegee* UC; winter, 1892 and 1893, *Franceschi* POM, UC, US; 1875, *Palmer 33* GH, US.

Hanna and Anthony (1923) state that goats have denuded the island. It is possible that this species has become extinct.

FIG. 5. *Marah oreganus*, *Brandegee* DS 7502 (left); *M. guadalupensis*, type, *Palmer* 33, 1875 GH (right).

3. Marah watsonii (Cogn.) Greene, Leafl. Bot. Obs. 2: 36. 1910. *Echinocystis muricatus* Kell. Proc. Calif. Acad. ser. 1, 1: 57. 1885, not *Marah muricatus* Kell., 1855. Type: vicinity of Placerville (did not survive the San Francisco fire of 1906). *Megarrhiza muricata* (Kell.) Wats. Proc. Am. Acad. 11: 139. 1876. *Echinocystis watsonii* Cogn. Monogr. Phan. 3: 819. 1881. *Micrampelis watsonii* Greene, Pittonia 2: 129. 1890.

The following topotype represents the author's concept of the species and may be taken as a lectotype until such time as some other specimen, historically with better claim to this status, may be located: Institute of Forest Genetics, 3 miles east of Placerville, El Dorado County, *Robbins 1057* (UC! photograph KMS! fig. 4).

Aerial stems from 1 the first year to 5 in older plants, 1–3 mm. in diam., 1–3 m. long, nearly glabrous with few scattered hairs, the internodes 3–12 cm. long; leaf blade orbicular, 3–8 cm. wide, almost as long, 5-cleft, the lobes heavily clavate, often further 2- or 3-lobed, apices of lobes obtuse (sometimes acute), some minutely mucronate, basal sulcus of blade 2 cm. deep, about half as wide, the margin entire or with occasional small teeth; petiole 2–5 (–7) cm. long, sub-glabrous; tendrils bifid or undivided, the peduncle 1–3 cm. long; staminate flowers 3–12 per raceme, the racemes 4–12 (–20) cm. long, the pedicels filiform, 10–15 mm. long, the calyx lobes lanceolate, 0.5 mm. long, to 0.4 mm. broad at lower part of base, the corolla campanulate, more closed than in *M. oreganus,* 5–6 (–8) mm. in diam., its tube 3–4 (–6) mm. long, greenish, especially when young, its limbs triangular-ovate, to 2.5–3 mm. long, not quite as wide at the base, obtuse, glandular-papillate on inner surface, the anther head cylindrical, to 1.33 mm. in diam., to 2.5 mm. long, the filament column to 1 mm. long, 0.67 mm. in diam.; pistillate flower with calyx lobes linear-subulate, to 1 mm. long and 0.75 mm. broad at base, the corolla 8–12 mm. in diam., its tube to 4 mm. long, its lobes to 5 mm. long and 3 mm. wide at base, the apices obtuse, the staminodia oblong, to 0.67 mm. long and 0.33 mm. wide, the stigma rounded, obconic, surface rather smooth, 3 mm. in diam., somewhat less thick, the style 0.5 to 1 mm. long, slightly wider than long, the ovary globose, tapering to a tip above when young, with few broad-based prickles; fruit globose, somewhat flattened at the two poles, 2–3 cm. in diam., polar axis 0.67 to 0.75 as long as diam., the spines usually 1 or more, weak, glabrous, 1–2 mm. long, near peduncle, the dark green meridional lines conspicuous, the coats thin, non-rigid when dry; peduncle (2.5–) 3–4 (–4.5) mm. long; seeds globose, 11–14 mm. in diam., 2– (1–4) per mature fruit, in 2 locules, slightly flattened away from the poles, greyish brown, mottled with a reticulum of dark lines, mature seeds outlined by an inconspicuous black band.

This is the most slender and least branched species of the genus.

Chaparral and woodland of the Upper Sonoran Life Zone of central and north central California (fig. 5).

Representative specimens seen. Amador County: 2.1 miles northeast of Plymouth, March 21, 1947, *Stocking 11* USC. Butte County: 8 miles north of Oroville, April 27,

FIG. 4. *Marah watsonii,* lectotype, *Robbins 1057* UC (left) ; *M. fabaceus* var. *agrestis, Stocking 31* USC (right).

1914, *Heller 11328* CAS, DS, UC, US; 0.9 mile west of Paradise on short-cut to Chico, April 17, 1947, *Stocking 28* USC. Calaveras County: Angels Camp, April 11, 1923, *Eastwood 11564* CAS, POM. Shasta County: Keswick, May 19, 1913, *Smith 234* CAS.

4. Marah fabaceus (Naud.) Greene, Leafl. Bot. Obs. 2: 36. 1910.

Aerial stems from 1 the first year to 20 in older plants, 3–7 m. long, 1–3 mm. in diam., slightly pubescent to sub-glabrous, internodes 7–10 cm. long; leaf blade sub-orbicular, 5–10 cm. long and wide; more or less deeply 5–7-lobed, the lobes less than one-half the leaf length, their apices acute or obtuse, occasionally mucronate, the basal sulcus of blade 1–3 cm. deep, one-half as broad to somewhat broader at opening, narrowing toward the base, or sometimes partially closed above, the blade surfaces glabrous to somewhat scabrous; petiole 3–6 cm. long; tendrils usually bifid, the peduncle 1.5–3 cm. long; staminate flowers in racemes or panicles 8–15 (–25) per raceme, the racemes 5–15 cm. long and panicles to 25 cm., the pedicels to 6 mm. long, the calyx teeth almost always lacking or if present, minute, the corolla rotate, (6–) 7–10 (–13) mm. in diam., 5–8-merous, cream or greenish-white, its tube (2.5–) 3–4 (–5) mm. long, its lobes unequal, deltoid or somewhat lanceolate, 1.5–2.5 (–3.5) mm. long, half as wide to not quite as wide at the base, with trichomes on margins and inner surfaces, the anther head short-cylindrical, 1.5–2 mm. in diam., 1–1.5 mm. thick, the filament column 0.67–1 (–2) mm. long; pistillate flower with corolla rotate, 5–7 (–12)-merous, 10–15 mm. in diam., its lobes unequal, 3–5 mm. long, about one-half as wide at the base, sub-acute, the staminodia lacking, the stigma discoid, 2 (–3) mm. in diam., 0.67–1 mm. thick, sessile or nearly so, the ovary globose below, tapering to a tip; fruit globose, 4–5 cm. in diam., densely spinose, the spines rigid, 12 mm. long, 1–2 mm. in diam. at the base, the carpels 4 with usually 1 ovule per carpel; peduncle 3–5 cm. long; seeds lenticular, oblong-obovoid, 18–24 mm. long, 15–20 mm. wide, 12–15 mm. thick, the hilum ridged, 5 mm. long, brownish-tan.

Key to Varieties

Spines less than 5 mm. long, somewhat soft; locules with mature seeds often 2 or 3; seeds seldom flattened laterally . . . . . a. var. *agrestis*

Spines more than 5 mm. long, rigid; locules with mature seeds usually 4; seeds commonly flattened laterally . . . . . b. var. *fabaceus*

4a. M. fabaceus var. **fabaceus.** *Echinocystis fabaceus* Naud. Ann. Sci. Nat. Bot. ser. 6, 12: 154. 1859. Type: Paris Botanical Garden from seeds obtained in California by Dr. Aube, *Naudin. Megarrhiza californica* Torr. in Wats. *pro parte*, Bot. Calif. 1: 241. 1876, excl. specim. *Bigelow*, Cocomungo. *Micrampelis fabacea* (Naud.) Greene, Pittonia 2: 129. 1890.

Fruits quite globose, thick walled; locules with mature seeds usually 4; spines more than 5 mm. long, rigid; seeds somewhat asymmetrical, flattened laterally.

Near coast of central California from Marin to Monterey counties, chiefly in Coastal Transition Life Zone (fig. 5).

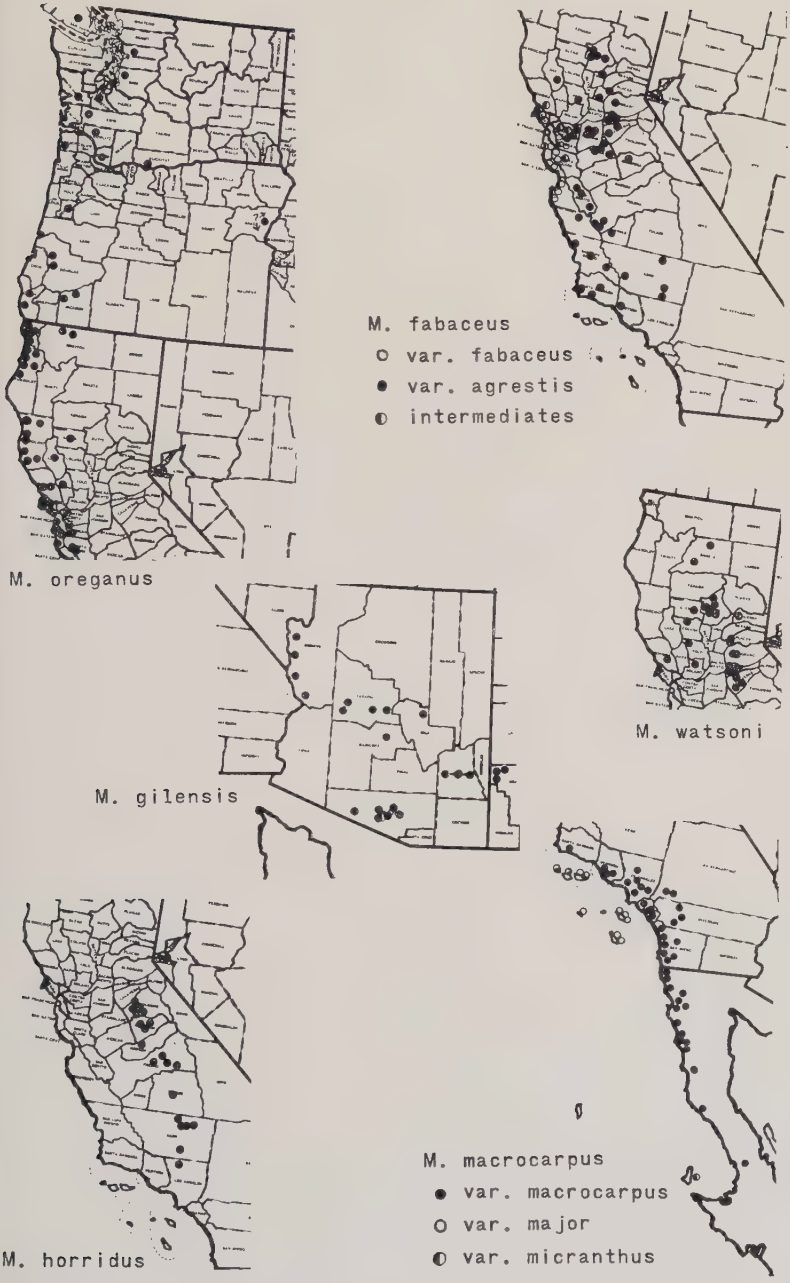

FIG. 5. Distribution maps of species of *Marah*.

Representative specimens seen. Marin County: wooded slope, Lone Pine Beach, Tomales Bay, July 25, 1932, *Schreiber 662* LA. Monterey County: Whaler's Knoll, Point Lobos State Park, Feb. 9, 1935, *Lee & Mason 9213* UC. Santa Clara County: foothills west of Los Gatos, March 12, 1904, *Heller 7262* GH, UC; Stanford University, April, 1903, *Elmer 4863* ARIZ, DS, POM. Santa Cruz County: 4 miles west of summit on Los Gatos-Santa Cruz highway, elev. 1,700 feet, May 11, 1947, *Stocking 34* USC.

There is definite intergradation between var. *fabaceus* and var. *agrestis* (fig. 5). Further collections of material bearing mature fruit will undoubtedly bring to light even more intermediates than now known.

Intermediate specimens seen. Contra Costa County: 1 mile west of Martinez, March 29, 1947, *Stocking 18* KMS; Nortonville hills, March 29, 1933, *Howell 10902* CAS. Santa Clara County: Milpitas, March, 1906, *Smith* ARIZ. Sonoma County: 1 mile west of Petaluma, March 29, 1947, *Stocking 19a* KMS.

4b. M. FABACEUS var. **agrestis** (Greene) comb. nov. *Micrampelis fabaceus var. agrestis* Greene, Fl. Fran. 236. 1891. No type specimen for Greene's variety has been located but he cites the plant as occurring on "open plains . . . of the valley of the San Joaquin." Until some other specimen, historically with better claim to this status may be located, the author designates the following specimen as lectotype: 1½ miles east of Linden, San Joaquin County, 25 April 1947, *Stocking 31* USC, (fig. 4).

Echinocystis inermis Congdon, Zoe 5: 134. 1901. Type: Sherlocks, Mariposa County, *Congdon* (UC 131976! photograph KMS!) *Marah inermis* Dunn, Kew Bull. 4: 153. 1913. *Echinocystis fabacea* var. *inermis* Jepson, Fl. Calif. 2: 554. 1936.

Echinocystis scabrida Eastw., Bull. Torrey Club 30: 500. 1903. Type: ". . . collected by Mrs. T. S. Brandegee in Fresno Co., Calif., at Zapato, [and] Chino Creek, Mar. 26, 1893, and also at Alcalde in the same region." *Mrs. T. S. Brandegee* (CAS! type number 354, photographs KMS!).

Similar to variety *fabaceus* except spines less than 5 mm. long, soft; seeds often 1–3, symmetrical, lateral edges rounded.

Common in Upper and occasional in Lower Sonoran Life zones of California, especially in the interior; along the coast only between points in San Luis Obispo and Ventura counties (fig. 5).

Representative specimens seen. Butte County: 9.6 miles from Paradise on Oroville road, elev. 250 feet, April 17, 1947, *Stocking 29* USC. Calaveras County: 3–5 miles east of Milton, April 25, 1947, *Stocking 32* USC. Fresno County: 2 miles west of Coalinga, April 2, 1947, *Stocking 20* USC. Kern County: between Rosamund and Mojave, April 30, 1927 *Abrams 11793* DS. Lake County: Clear Lake Park, May 16, 1938, *Eastwood & Howell 5572* CAS, GH. Santa Barbara County: 5 miles south of Surf, April 14, 1929, *Ferris 7579* DS, UC. Ventura County: Murietta Canyon, Ventura River basin, elev. 2,500–3,000 feet, April 26, 1947, *Pollard* CAS.

The Bigelow (Knights Ferry) collection cited by Watson (1876, p. 241) has not been located, but one can assume that it belongs in *M. fabaceus* var. *agrestis*.

The Santa Clara River valley in Ventura County, the southern side of the Tehachapi Mountains, and the Mojave Desert form both the southern

boundary for *M. fabaceus* var. *agrestis* and the northern boundary for *M. macrocarpus* var. *macrocarpus*.

5. MARAH HORRIDUS (Congdon) Dunn, Kew Bull. 4: 151. 1913. *Echinocystis horrida* Congdon, Erythea 7: 184. 1900. Type: ". . . foothills of Mariposa County, California," *Congdon* (UC 28933! photographs KMS! fig. 6: isotypes UC 131939! UC 131940!).

Aerial stems from one the first year to 15 on older plants, 1–4 m. long, 2–4 mm. in diam., sparsely puberulent; leaf blade orbiculate, 10–15 cm. broad, not quite as long, usually rather deeply 5- or 7-lobed, the apices of lobes acute or obtuse, the basal sulcus of blade to 4 cm. deep, much narrower or as broad, blade margin sinuate-dentate to sub-entire, the upper surface more or less scabrous, lower surface less so; petioles 3–8 cm. long; tendrils bifid, the peduncle (2–) 3–5 cm. long; staminate flowers in racemes or panicles, with 5–12 flowers per raceme, the racemes 7–16 (–23) cm. long, pedicels 5–15 mm. long, the calyx lobes 0–3, subulate-lanceolate, to 0.7 mm. long and 0.33 mm. wide at base, the corolla campanulate, 10–12 (–15) mm. in diam., its tube 5–7 mm. long, its lobes as long, 3–4 mm. wide at base, obtuse, white, the anther head cylindrical, 2–2.5 mm. in length and diam., the filament column 2–2.5 mm. long, 1 mm. in diam.; pistillate flower 13–17 mm. in diam., with calyx lobes 1 mm. long, filiform, the corolla lobes broadly lanceolate, 7–9 mm. long, 3–4 mm. wide at base, the staminodia 1–1.5 mm. long, the stigma to 3.5 mm. in diam., to 2 mm. thick, the style 1–1.5 mm. long, the ovary oblong-ellipsoidal, slightly pointed at each end, with spines conspicuous, the carpels 4 (–6 or –8), the ovules usually 3 per carpel; fruit oblong-ellipsoidal, 9–15 cm. long, 6–9 cm. in diam., very spinose, the spines 5–35 mm. long, 3–7 mm. wide at the base, variable lengths on one fruit; peduncle 4–6 cm. long; seeds lenticular, oblong-obovoid, 26–32 mm. long, 15–18 mm. wide, 13–15 mm. thick at thicker end, light olive, some seeds encircled by slight ridge, the ridge grooved at maturity, the hilum ridged, 5 mm. long.

Upper Sonoran Life Zone, foothills of Sierra Nevada and Tehachapi Mountains, California, from Tuolumne River to Lake Hughes in Los Angeles County (fig. 5).

Representative specimens seen. Fresno County: about 2 miles east of Dunlap, April 4, 1947, *Stocking 22* USC; Pine Flat Dam, 1 mile west, *Stocking 53* KMS. Los Angeles County: Lake Hughes, *Johnstone* USC. Mariposa County: 2 miles west of El Portal, elev. 2,000 feet, April 9, 1941, *Rose 41105* CAS, GH. Tuolumne County: chaparral, Rawhide Hill, elev. 1,300 feet, April 11-16, 1919, *Ferris 1469* DS, POM, UC, US.

6. MARAH MACROCARPUS (Greene) Greene, Leafl. Bot. Obs. 2: 36. 1910.

Aerial stems from 1 the first year to 10 in older plants, 1–7 m. long, 2–4 mm. in diam., deeply striated, the internodes 5–10 cm. long; leaf blade sub-orbicular, 5–30 cm. wide, not quite as long, the lobes deep, the apices acute or obtuse, surfaces of blade more or less scabrous above, his-

pid beneath, the basal sulcus deep; petiole 2–10 (15) cm. long; tendrils usually bifid, sometimes trifid, the peduncle to 12 cm. long; staminate flowers in racemes or panicles, 5–15 (–25) flowers per raceme, the inflorescences 5–20 (–40) cm. long, the pedicels 2–10 (–20) mm. long; staminate flower with calyx lobes 5 up to 2.2 mm. long, to 0.8 mm. broad at base, deltoid to linear-lanceolate, sometimes obsolete, the corolla cup-shaped, 3–30 mm. in diam., white, its lobes ovate to oblong-ovate (1–) 3–10 (–12) mm. long, 2–3 (–5) mm. wide at base, with apices obtuse, the anther head sub-globose, 1–1.5 (–2) mm. in diam., the filament column 0.8–1.5 mm. long; pistillate flower with calyx lobes sub-obsolete or deltoid and to 0.67 mm. long, the corolla cup-shaped, 5–24 mm. in diam., its lobes oblong-ovate, 5–8 (–10) mm. long, 3–5 mm. wide at base, with apices obtuse, the staminodia scale-like or lacking, 0.6 mm. in diam., not quite as wide on some, the stigma 2–3.33 mm. in diam., not quite as thick, the style to 0.6 (–1.33) mm. long, the ovary oblong with carpels 4; fruit cylindrical, beaked, (5–) 8–12 cm. long, (4–) 6–9 cm. in diam., densely spiny, the spines flattened, 5–30 mm. long, 1–3 mm. wide at base, with trichomes; peduncles to 4 cm. long; seeds oblong, somewhat flattened and angular-ovoid or sub-globose; 12–33 mm. long, (8–) 9–25 mm. wide, 6–14 mm. thick, olive-brown (some races reddish-brown) with a conspicuous, more or less dark equatorial line.

Key to Varieties

Staminate flowers 14–30 mm. in diam.; seeds 28–33 mm. long . . b. var. *major*
Staminate flowers less than 14 mm. in diam.; seeds less than 21 mm. long.
  Staminate flowers 8–13 mm. in diam.; seeds 15–20 mm. long . a. var. *macrocarpus*
  Staminate flowers 3–6 mm. in diam.; seeds 10–13 mm. long . c. var. *micranthus*

6a. M. MACROCARPUS var. **macrocarpus.** *Megarrhiza californica* Torr. in Watson, Bot. Calif. 1: 241. 1876, as to the *Bigelow*, Cocomungo [Cucamonga, San Bernardino County?] specimen. *Echinocystis macrocarpa* Greene, Bull. Calif. Acad. 1: 188. 1885.

Micrampelis leptocarpa Greene, Pittonia 2: 282. 1892. Type: "the Colorado Desert, in southern California," *W. G. Wright*. (None of the original specimens from which Greene drew his descriptions have been positively located. This is a very questionable entity.) *Marah leptocarpa* (Greene) Greene, Leafl. Bot. Obs. 2: 36. 1910. *Echinocystis macrocarpa* var. *leptocarpa* (Greene) Wright, Muhlenbergia 3: 125. 1907.

The following topotype represents the author's approximate concept of the species and may be taken as a lectotype until such time as some other specimen, historically with better claim to this status, may be located: vicinity of San Bernardino, California, *S. B. Parish 3633* (US! photographs KMS! fig. 6, isotype GH!).

Leaf blade 5–10 cm. wide, petiole 2–7 cm. long; tendrils to 5 cm. long; staminate racemes 5–15 cm. long, pedicels 4–10 mm. long; staminate flower 9–12 mm. in diam., the calyx lobes obsolete to short subulate or deltoid, the corolla lobes 3–4 (–5) mm. long, the anther head diam.

FIG. 6. *Marah horridus*, type, Congdon UC 28053 (left); *M. macrocarpus* var. *macrocarpus*, lectotype, Parish 3633 US (right).

0.8–1.25 mm., filament column 0.6–1.25 mm. long; pistillate flower 15–20 mm. in diam. with calyx lobes obsolete or very reduced, the corolla lobes 5–7 mm. long, the staminodia lacking to 0.4 mm. long, the stigma 2–3 mm. in diam., the style to 0.6 mm. long; fruit 8–10 cm. long, 6–9 cm. in diam.; seeds 15–20 mm. long, 12–18 mm. wide, 11–14 mm. thick, brownish tan.

Southern California, Northern District of Baja California, Mexico, and coastal islands to the west (fig. 5).

Representative specimens seen. California. Los Angeles County: 2 miles north of Claremont, March 3, 1932, *Wheeler 455* DS. Ventura County: Foothill Trail, Ventura River basin, March 25, 1945, *Pollard* CAS. Mexico. Baja California. Northern District: Cabo Punta Banda, south arm of Todos Santos Bay, Feb. 24, 1930, *Wiggins 4231* ARIZ, CAS, DS, GH, US; 2–5 miles north of Hamilton Ranch, Santo Domingo, March 2, 1930, *Wiggins 4296* CAS, LA, POM, US; Santa Catarina Landing, March 10, 1930, *Wiggins 4436* LA, POM, UC, US.

Intergradation between var. *macrocarpus* and var. *major* is suggested by several specimens from the Channel Islands. Collections have not been extensive enough to show complete intergradation clearly. In Baja California var. *macrocarpus* may intergrade with var *micranthus* (*Wiggins 4436*).

It is quite interesting to note that a line along the Santa Clara River in Ventura County, through Lake Hughes in Los Angeles County and thence eastward marks not only the northern limit of *M. macrocarpus,* but also the southern limits of both *M. fabaceus* var. *agrestis* and *M. horridus*.

6b. M. macrocarpus var. **major** (Dunn) comb. nov. *M. major* Dunn, Kew Bull. 4: 151. 1913. Type: "S. California Islands. San[ta] Catalina, San Clementi[e], San Nicholas . . . common in moist canyons . . . white flowers . . . roots as large as small barrels," *Trask 281* (US! photographs KMS!, fig. 7; isotype US!).

Leaf blades (10–) 15–25 (–30) cm. in diam.; staminate flowers (14–) 16–30 mm. in diam., the calyx lobes linear-lanceolate, 2–2.2 mm. long, 0.6–0.8 mm. broad at the base; pistillate flowers 20–24 mm. in diam., the calyx lobes deltoid, 0.67 mm. along each side; seeds (22–) 28–33 mm. long, (17–) 21–25 mm. wide, 12–14 mm. thick; other vegetative and reproductive parts of this variety correspondingly large.

On all of the larger Channel Islands of California from San Miguel in the north to San Clemente in the south (fig. 5).

Representative specimens seen. San Clemente Island, Middle Ranch, Feb. 16, 1941, *Moran 573* DS; shaded slope, east coast, April 11, 1923, *Munz 6779* GH. San Miguel Island: April 10, 1930, *Munz & Crow 11,810* POM. San Nicholas Island: April, 1901, *Trask* US. Santa Catalina Island: Avalon, March, 1901, *Trask* US. Santa Cruz Island: Pelican Bay, April 26, 1930, *Abrams & Wiggins 64* CAS, GH. Santa Rosa Island: June, 1888, *Brandegee* UC.

6c. M. macrocarpus var. **micranthus** (Dunn) comb. nov. *M. micranthus* Dunn, Kew Bull. 4: 150. 1913. Type: Cedros Island, *Rose 16159* (US! photographs KMS! fig. 7).

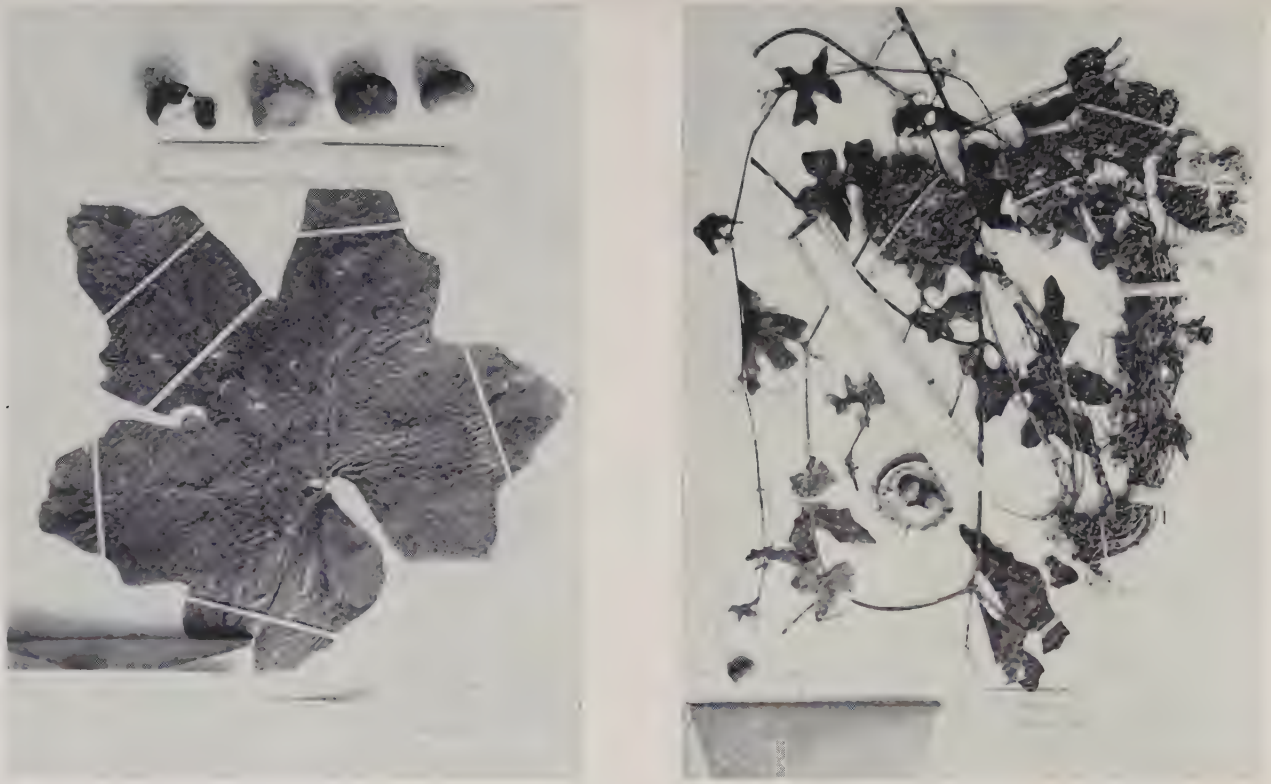

FIG. 7. *Marah macrocarpus* var. *major*, type *Trask 281* US (left) . *M. macrocarpus* var. *micranthus*, type, *Rose 16159* US (right).

FIG. 8. *Marah gilensis,* type, *Greene* ND.

Staminate flowers 3–6 (–8) mm. in diam.; pedicels 2–4 mm. long; fruit 3–5 (–6) cm. long; seeds 12–13 mm. long, 9–10 mm. wide, 6 mm. thick; other dimensions in proportion.

Known only by the two following collections from Cedros Island, off the west coast of Baja California, Mexico, 28° N.: *Rose 16159,* March 12, 1911, US; and *Brandegee,* April, 1897, UC 102131, 102133, 102134 (fig. 5).

7. MARAH GILENSIS (Greene) Greene, Leafl. Bot. Obs. 2: 36. 1910. *Megarrhiza gilensis,* Greene, Bull. Torrey Club 8: 97. 1881. Type: "the canyon of the Upper Gila in Grant County, New Mexico, within fifteen miles of the dividing ridge between the Pacific and Atlantic slopes." . . .

Cañon of the Gila, April 30 [20?], 1881, *Edward L. Greene* (photographs ND! KMS! fig. 8; possible isotypes GH! photographs ND! KMS!). *Echinocystis gilensis* Greene, Bull. Calif. Acad. 1: 189. 1885. *Micrampelis gilensis* Britt. Trans. N. Y. Acad. 8: 67. 1889.

Stem slender, 2(–3) mm. in diam., puberulent to sub-glabrous, internodes 5–15 cm. long; leaf blade orbicular, 4–10 cm. in diam., deeply 5–7-lobed, the lobes to 5–7 times as long as broad, central apex acute, others acute to obtuse; basal sulcus of blade to 25 mm. deep., 0.33–0.5 as broad, the margins entire or sometimes irregularly and broadly dentate, upper surface scabrous, lower slightly so; petioles 2–4 cm. long; tendrils unbranched or bifid, peduncle 2–2.5 (–3) cm. long; staminate flowers in racemes, seldom in panicles, 10–20 flowers per raceme, the racemes 15–25 cm. long, the pedicels 2–5 mm. long, the calyx lobes almost obsolete, the corolla rotate, 6–10 (–11) mm. in diam., the corolla tube 2–4 mm. in diam., its lobes deltoid to lanceolate, 3–3.5 mm. long, 2–3 mm. wide at the base, obtuse or acute, the margins and inner surfaces glandular-punctate, the anther head somewhat triangularr in cross-section, 1–1.6 mm. in diam., about one-half as thick, filament column 1 mm. long, slender; pistillate corolla rotate, 10–12 mm. in diam., the lobes 3–4 mm. long, 1–1.5 mm. wide at base, with apices obtuse or acute, the staminodia very inconspicuous, less than 1 mm. long, the stigma 2–2.5 mm. in diam., 1–1.25 mm. thick, the style 0.5–0.8 mm. in diam., not quite as long, the ovary globose with carpels and ovules usually 4, spines conspicuous; fruit globose with a rather persistent beaked apex, 26–32 mm. in diam., the spines rather dense, stout, 2–3 (–5) mm. long; peduncle 8–12 mm. long; seeds ovoid-lenticular, 14–16 mm. long, 10–12 mm. wide, 7–10 mm. thick, dark brownish-olive, encircled by a grooved ridge, bottom of groove dark.

Arizona and southwestern New Mexico (fig. 5).

Representative specimens seen. Arizona. Mojave County: Chloride, elev. 4,500 feet, April 14, 1903, *Jones* DS, POM, US. Pima County: Ajo Mountains, Ajo, April 19, 1942, *Cooper 636* AHFH; shallow gorge, Coyote Mountains, elev. 4,000 feet, Feb. 4, 1945, *Phillips 2597* ARIZ, CAS, GH, US. Yavapai County: Congress Junction, elev. 3,000 feet, May 2, 1903, *Jones* CAS, DS, POM, US. New Mexico. Grant County: Burro Mountains, May, 1880, *Rusby 141* UC, US.

College of the Pacific,
Stockton, California

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OBSERVATIONS ON PRASIOLA MEXICANA, A FRESHWATER ALGA OF UNKNOWN RELATIONSHIPS

Herbert F. Copeland

The observations upon *Prasiola mexicana* J. Agardh which are here presented were made in the expectation that they would clarify the relationships of this organism. This expectation has not been fulfilled.

Prasiola mexicana produces thin green thalli, of small to moderate size, on stones in mountain streams. In conventional classification it is placed in or near the family Ulvaceae, to which plants, however, it is not closely similar in microscopic structure. The cells of *Prasiola* (their dimensions are of the order of 5 to 10μ) become separated in a colorless matrix. They divide in three planes. A cross section of the thallus shows ordinarily two layers of octettes of cells. Continuing division may produce columns of several cells. These features of the structure are shown in the illustrations of Setchell and Gardner (1920). In living material the protoplast appears to consist principally of a single bright green plastid lying in the middle of the cell and connected to the cell membrane by radiating strands (fig. 1, a). Setchell and Gardner suggested the possibility that *Prasiola* may not belong naturally with the green algae, but with the primitive red algae. According to Kylin (1930), however, the pigmentation is that of green algae and higher plants.

The material studied was collected in Butte Creek at Jonesville, Butte County, California, at an altitude of about 1500 m. Since nuclear and cell division occur in many organisms at particular times of the day, material was fixed at intervals of from one to two hours during one day and night. Portions of each collection were fixed respectively in iron acetocarmine and in FAA. A part of the material in FAA was stained as whole mounts with Heidenhain's haematoxylin; another part was dehydrated, imbedded, and sectioned at 10μ. Some of the sections were stained with Heidenhain's haematoxylin, and others with other stains, including basic fuchsin applied after several minutes exposure to warm normal hydrochloric acid.

No difference was observed in the condition of the cells fixed at different times; in particular, an abundance of newly divided cells was present in every collection. The sectioned material stained with Heidenhain's haematoxylin showed the internal structure most clearly: other techniques gave the same results as this, or else failed to show the internal structure.

As protoplasts stained in Heidenhain's haematoxylin are destained in iron alum, four concentric parts become distinguishable. In order from outside to inside, these are as follows (fig. 1, b, c, d).

1. A narrow superficial layer is destained promptly.

2. Within the foregoing there is a thicker layer which is more resistant to destaining. After very brief destaining it appears as a solid black mass

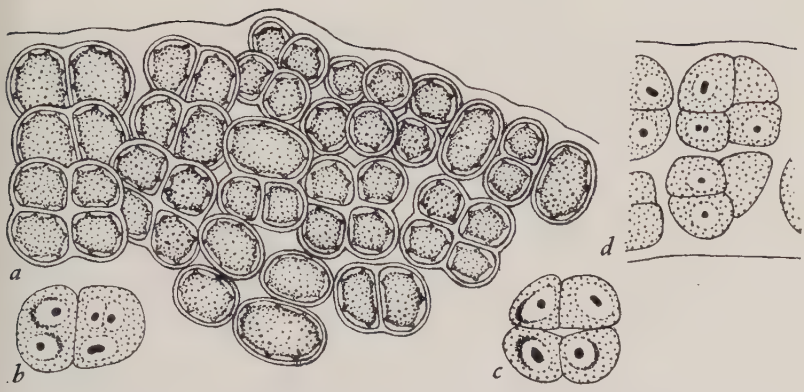

FIG. 1. *Prasiola mexicana*. *a*, living cells in surface view; *b*, *c*, *d*, stained cells, *b*, *c*, in surface view, *d*, in a cross section of the thallus; all × 1000.

nearly filling the cell. Further destaining decolorizes it gradually from without inward; eventually, it becomes indistinguishable from the superficial layer. This body is believed to be the plastid.

3. Inside of the plastid there is a fairly extensive area (here called the "clear space") which is more promptly destained. No definite membrane has been seen at the boundary of the clear space.

4. In the middle of the clear space there is a granule (here called the "central granule") about 0.5μ in diameter. It is the most resistant to destaining of all parts of the cell. It is sometimes slightly irregular in outline. In some preparations one can see vague strands radiating from it. No internal structure has been seen.

At least one clear space and one central granule are present in every cell. In many cells, the central granule is elongate. Rarely, two central granules can be found in one clear space; usually, if a cell contains two or more central granules, even quite close together, they lie in separate clear spaces. It appears that the central granule divides by constriction and that the clear space divides very promptly after it. Constriction of the protoplast is less prompt, and may be delayed until four or more clear spaces and central granules are present.

According to these observations, cells of *Prasiola mexicana* have no nucleus in the proper sense of the word: no structure limited by a membrane, and whose division involves the appearance and division of definite chromosomes, was seen. Nothing was seen of the nature of the parietal granule, apparently a primitive nucleus, which has been described in the lower red algae, in *Porphyridium* by Lewis and Zirkle (1920), in *Porphyra* by Ishikawa (1921), and in *Bangia* by Dangeard (1927). The structure is not that of the blue-green algae. Except for the plastid, it is very much like bacterial structure as it is currently understood (Robinow, 1942, 1949; Tulasne and Vendrely, 1947; Hillier, Mudd,

and Smith, 1949). The relationships of *Prasiola* remain altogether obscure.

Sacramento Junior College,
Sacramento, California.

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A NEW SPECIES OF BOUVARDIA (RUBIACEAE) FROM BAJA CALIFORNIA, MEXICO

Annetta Carter

During the past sixty or seventy years the flora of Baja California, Mexico, has become reasonably well known in the vicinity of anchorages along the Pacific Ocean and Gulf of California, in the mountains of the north and some of those of the Cape Region, and along "El Camino Nacional," as the main route of travel the length of the peninsula is now officially known. Whenever a botanist manages to get off the beaten track, however, he is quite apt to find plants of special interest. Arroyo del Salto, which empties into the Gulf east of La Paz near Las Cruces in the Cape Region, is such a place. Here, where a granite dike forms a dam across the upper reaches of the deep and narrow canyon, is an oasis of tall palms (*Erythea Brandegeei* Purpus) and an abundance of such moisture-loving herbaceous plants as *Samolus ebracteatus* H.B.K., *Bacopa Monnieri* (L.) Pennell, and *Cyperus*. On the drier talus slopes and cliffs, in addition to the usual *Lysiloma candida* Brandegee, *Jatropha cinerea* (Orteg.) Muell., *Cyrtocarpa edulis* (Brandegee) Standl., and *Fouquieria peninsularis* Nash, I found the *Bouvardia* described below as well as the

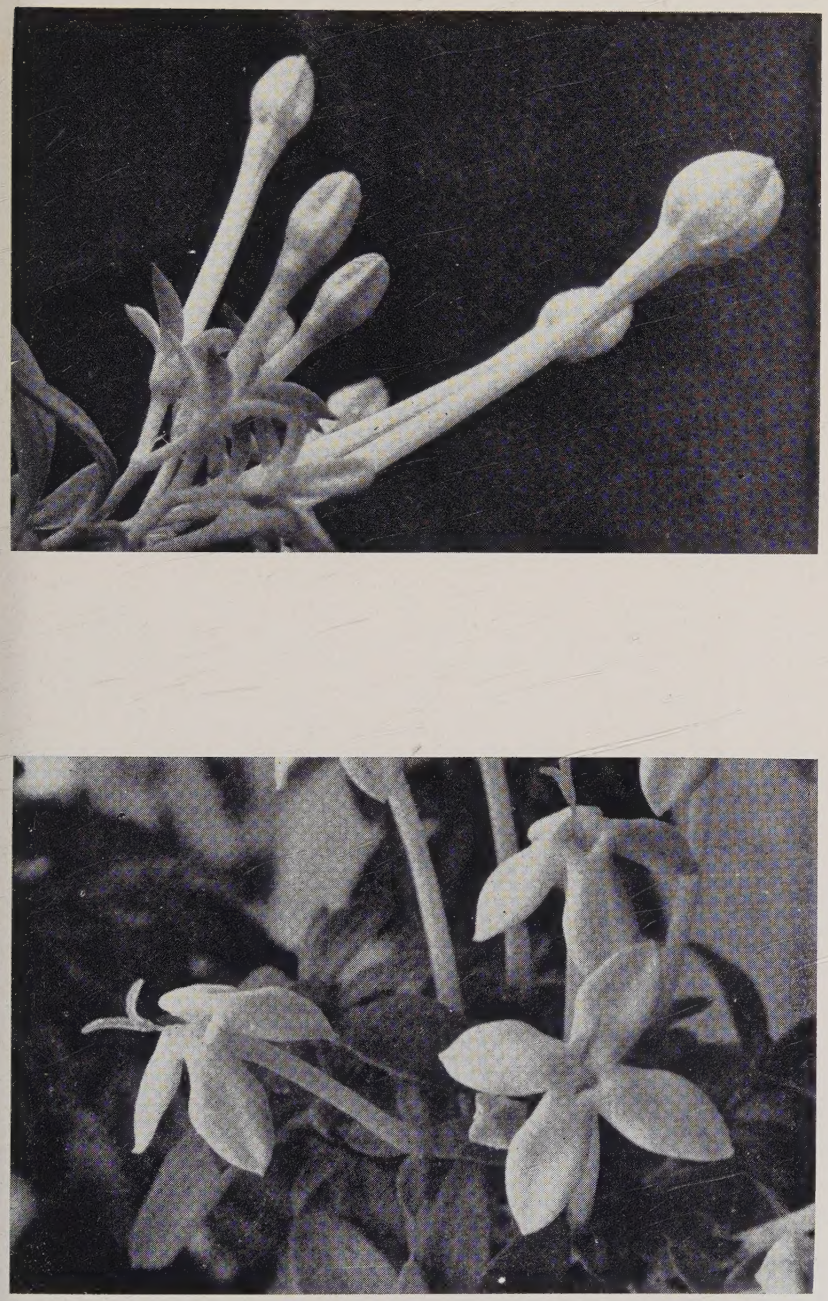

FIG. 1. Inflorescences of *Bouvardia Alexanderae:* upper, valvate buds; lower, from plant having flowers with styles exserted and stamens included. All × 2.

delicate annual, *Drymaria debilis* Brandegee, a species not previously reported from south of La Purísima (ca. latitude 26°N.), and *Dudleya nubigena* (Brandegee) Br. & Rose, known before only from the type locality in the Sierra de la Laguna.

Bouvardia Alexanderae sp. nov. Planta perennis lignosa scabrida foliis oppositis vel plerumque ternatis lineari-lanceolatis apice acutis 15–45 mm. longis 3–10 mm. latis floribus in cymis terminalibus 5–12-floris dispositis hypanthio obconico 2–3 mm. longo 3 mm. lato calycis lobis lanceolato-linearibus acutis crassis patentibus 4–5 mm. longis corolla hypocraterimorpha alba tubo gracili 2.5–3.5 cm. longo ejus lobis oblongis plus minusve acutis 8–10 mm. longis 4–5 mm. latis staminibus inclusis vel exsertis heterostylis stylo exili stigmate bifido 4–5 mm. longo ovario biloculari placentis peltatis crassis prope septi basem affixis ovulis numerosis ad perpendiculum dispositis capsula globosa fissura septo ad perpendiculum dehiscente seminibus exalatis angulatis diametro 1 mm. vel minoribus.

Type. Steep granite talus, Arroyo del Salto (latitude 24°12′N., long. 110°7.5′W.), east of La Paz, Baja California, Mexico, March 30, 1949, *Annetta Carter 2577* (UC 985926).

Woody perennial 3–6 dm. tall, stems terete, scaberulous, epidermis exfoliating on older parts, the internodes 10–25 mm. long; leaves 15–45 mm. long, 3–10 mm. wide, opposite, or occasionally in whorls of three, linear-lanceolate, acute at apex, sessile or gradually tapering to a short petiole, glabrous or slightly scaberulous on margins and midrib, the venation, except for the midrib, obscure; stipule sheath hyaline-membranous bearing several slender, hyaline teeth up to 2 (–3) mm. long; flowers in a terminal 5–12-flowered cyme on pedicels up to 1 cm. long, the pedicels with a hyaline, toothed scale at the base and occasionally below the hypanthium; hypanthium obconic, slightly quadrangular, 2–3 mm. long, 3 mm. broad, glabrous or slightly scaberulous; calyx lobes 4, lance-linear, acute, 4–5 mm. long, 1–1.5 mm. wide near base, 0.75–1 mm. thick, spreading, glabrous or slightly scaberulous, the sinus between the calyx lobes bearing one or two short hyaline teeth; flowers fragrant; corolla salverform, white (fading to pale rose) with a tint of rose dorsally on the midvein of the lobe, the tube slender, 2.5–3.5 cm. long, throat ca. 2 mm. in diameter, the lobes oblong, acutish, 8–10 mm. long, 4–5 mm. broad; stamens borne either at mouth of throat and exserted or at the base of the throat where they are included and nearly sessile, the filaments of the exserted stamens 1.5–2.5 mm. long; anthers 2–3 mm. long, versatile, yellow or black; heterostylic, style slender, stigma 4–5 mm. long, bifid; ovary inferior, two-celled, placenta swollen, peltate, attached near base of septum and bearing numerous crowded and vertically placed ovules; capsule globose, slightly two-lobed, 4 mm. broad and as high, dehiscing by an apical slit at right angles to the septum; seeds up to 1 mm. in diameter, angular, finely reticulate, wingless.

FIG. 2. *Bouvardia Alexanderae: a,* habit, × ½; *b,* seeds, × 15; *c,* dehisced capsule, × 5; *d* and *e,* corollas split longitudinally to show heterostyly, × 1½; *f,* calyx (showing thick spreading sepals with hyaline teeth in the sinuses), young capsule, and hyaline tooth on pedicel, × 2. Drawings by Emily Patterson Reid.

Because of its wingless seeds, *B. Alexanderae* keys to the genus *Houstonia* where it is not at all at home; in all other characters it fits into *Bouvardia,* where it falls in the section of the genus having large, white, salverform corollas with long tubes. Its 5–12-flowered compact cymes readily distinguish it from all of the closely related species: *B. induta* (Robinson) Standley, *B. Langlassei* Standley, *B. erecta* (DC.) Standley, *B. Karwinskyi* Standley, *B. glabra* Polak, *B. latifolia* Standley, and *B. longiflora* (Cav.) HBK. In addition, the linear-lanceolate leaves distinguish *B. Alexanderae* from all of its close relatives except *B. Karwinskyi* and *B. erecta.* Of these, *B. Karwinskyi* is described as a shrub 4–5 feet tall with long (15–26 mm.), linear calyx lobes and narrow, seemingly whorled leaves, while *B. erecta* is a divaricately, often rigidly branched, low shrub with 1–3-flowered cymes and winged seeds. *Bouvardia glabra* and *B. longiflora* also have winged seeds. This character has not been ascertained for the other above-mentioned species because of the lack of fruiting material.

No other species of *Bouvardia* are known to occur in Baja California, nor have the above-mentioned, closely related species been collected in the states of Sonora and Sinaloa on the opposite shore of the Gulf of California.

Bouvardia Alexanderae is named in memory of Miss Annie M. Alexander, who in 1947 invited me to accompany her and Miss Louise Kellogg on an expedition covering the length of the peninsula, thus initiating my field work of successive years in Baja California. She assisted generously in the financing of the 1949 trip during the course of which I collected this plant. In 1947 Miss Alexander, a keen and painstaking collector and an inspiring field companion, contributed her full share of work to the expedition and, although in her eightieth year, endured with cheerful equanimity the rigors of three months of rough travel and camping in the peninsula.

For the loan of herbarium specimens I wish to express my appreciation to the curators of the United States National Museum and the Chicago Natural History Museum. For fresh flowering material which served as a basis for the illustrations and certain details of the description, I am indebted to Mr. Frank F. Gander of Escondido, California, who, in his native plant nursery, grew plants from the seed that I provided. Mr. Gander (correspondence) reported that the plants bloomed profusely the first year, thrived in the hot, dry summer climate, withstood winter temperatures as low as 26°F., exhibited a tolerance to "hard" water, and did not seem to be attractive to rabbits. Because of its abundance of fragrant white flowers, its long blooming period, and its hardiness, *Bouvardia Alexanderae* may well prove to be a desirable garden plant in the Southwest.

Department of Botany,
University of California, Berkeley.